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INVITED RESEARCH OPINION

Vapour is the principal source of water imbibed by seeds in unsaturated soils

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Abstract

The assumption that seeds imbibe most of the water required for germination as liquid through seed-to-soil contact has been a dominant theme in germination research and seeding technology. Under most conditions, seeds are also exposed to water vapour during imbibition, but the relative contributions of liquid and vapour are difficult to assess. In water uptake models that include vapour, procedures used to estimate potential vapour imbibition have under-appreciated the effect of distance on diffusion rate. At the same time, the amount of seed-to-soil contact and the liquid bridge from soil water to the seed tend to be greatly overestimated, considering the soil water contents often found in the field. Most researchers have recorded an approximately equal time to germination at soil water contents ranging from field capacity to nearly permanent wilting point, and little response to bulk density, soil type or seed–soil contact. While hydraulic conductivity decreases by several orders of magnitude as soil water content, bulk density and seed-contact decrease, relative humidity remains near 100%. There are several experiments demonstrating timely germination in water vapour alone. The combined evidence contradicts the assumption that seed–soil contact is important for imbibition of water by seeds. Water vapour should be considered the primary source of water for seeds in unsaturated soils.

Keywords: germination, hydraulic conductivity, imbibition, seed–soil contact, water vapour

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Introduction

The importance of seed-to-soil contact has been emphasized for a long time in the water relations of seeds. Agriculturalists and others concerned with germination and growth of seeds often assume that the predominant source of imbibed water is contact with liquid water films on soil particles. However, it is difficult to measure transfer of liquid water from soil to seed, and especially difficult to separate this from the absorption of water as vapour. While seeds can be placed in liquid water and the rate of imbibition measured, it is deceptively difficult to create a laboratory set-up where water vapour is supplied at an unlimited rate. It is impossible to place seeds in an environment where soil, water and air exist, but without water vapour. As a result, we have a poor understanding of the relative contributions of liquid and vapour to seed imbibition.

Here, some common misconceptions are noted that appear to have hampered imbibition research, and evidence is presented that water vapour plays a major role in seed germination and probably other plant and soil phenomena. This discussion considers conditions where soil is not near saturation. Soil is usually seeded when dry enough to support the weight of humans or tractors, and to be worked without excessive plasticity, puddling and compaction, and yet often the soil is still moist enough to produce rapid germination and growth without additional rain or irrigation.

The seed environment in the field is extremely complex, varying over time and even with time of day. Depth of seeding, weather and soil conditions, species and condition of the seed all determine whether and how quickly germination and emergence occur. But this does not prevent the drawing of conclusions regarding the relative roles of liquid and vapour transport in imbibition of water by seeds in unsaturated soil.

Behaviour of liquid water in soil

Soils with different textures and compositions differ widely in the amount of water they can hold. Soil matric potential is a measure of the tension with which water is held on the surface of soil particles. In a particular soil, matric potential is a function of soil water content; the drier the soil, the greater the tension. The responses of plants and other biota, as well as many physical traits of soil, are closely related to matric potential. Since the attraction of water to the surface of a soil particle reduces its energetic potential relative to a free, pure body of water, the potential of soil water becomes more negative as a soil dries, and the units of matric potential are properly expressed as negative numbers. For convenience, however, soil water potential is sometimes expressed without the negative sign and referred to as soil water tension or suction, with the understanding that increasing (more positive) tension actually refers to decreasing (more negative) water potential.

Hydraulic conductivity is a measure of the rate at which water can move in a soil. Conductivity decreases rapidly as a soil dries. Table 1 shows an example of the relationship between matric potential and hydraulic conductivity. The relationship is exponential and can only be graphed using log scales on both axes, thus obscuring the drastic reduction in water conductivity as water content and matric potential decrease. For example, a very moist, but well-drained, soil at 'field capacity' (generally assumed to be around −0.03 MPa) and the same soil at −0.5 MPa (somewhat moist and still supporting healthy plant growth) might differ in hydraulic conductivity by a factor of 600.

Attempts to model liquid imbibition

Since germination is vital in establishing crops, and is also a factor in ecological fitness in natural settings and weed ecology, many researchers have been interested in the environment around a seed and its effect on the rate of germination. Liquid water transfer from soil to seed has been assumed to be the prime path for uptake during imbibition (see references in Table 2), so much research has centred on the relationship between hydraulic conductivity (by varying water content/matric potential) and germination rate, sometimes in combination with other factors, such as the extent of

Table 1. Water potential, equilibrium relative humidity (RH) and corresponding filled capillary size (based on Papendick and Campbell, 1981), and an example of hydraulic conductivity and volumetric water content for a fine-textured Geary silt loam (Hanks, 1965). In a medium-textured soil, the volumetric water contents might range from 0.40 to 0.05 $cm^3\,cm^{-3}$, with hydraulic conductivity at saturation of over 100 $cm\,d^{-1}$

Common terminology	Matric potential (MPa)	RH at 20°C	Capillary diameter (mm)	Hydraulic conductivity[a] ($cm\,d^{-1}$)	Volumetric water[a] ($cm^3\,cm^{-3}$)
Saturated	0	1.0000	∞	9.5000	0.46
	−0.0001	1.0000	2.908000	9.0000	0.46
	−0.0002	1.0000	1.454000	8.8000	0.45
	−0.0005	1.0000	0.582000	7.9000	0.44
	−0.0010	1.0000	0.291000	7.3000	0.44
	−0.0020	1.0000	0.145000	6.1000	0.42
	−0.0050	1.0000	0.058200	2.2000	0.38
	−0.0100	0.9999	0.029100	0.8700	0.35
	−0.0200	0.9999	0.014500	0.2900	0.32
Field capacity	−0.0330	0.9998	0.008790	0.1200	0.30
	−0.0500	0.9996	0.005820	0.0530	0.29
	−0.1000	0.9993	0.002910	0.0120	0.26
	−0.2000	0.9985	0.001450	0.0025	0.23
	−0.5000	0.9963	0.000582	0.0002	0.19
	−1.0000	0.9926	0.000291		
Permanent wilting point	−1.5000	0.9890	0.000190		
	−2.0000	0.9853	0.000145		
	−5.0000	0.9637	0.000058		
	−10.0000	0.9288	0.000029		
	−50.0000	0.6906			
Air dry	−100.0000	0.4776			
	−500.0000	0.0247			
Oven dry	−1000.0000	0.0006			

[a] Example of hydraulic conductivity and volumetric water content. Soils vary widely but always demonstrate an exponential decrease in conductivity with decreasing water content.

seed–soil contact and bulk density of the soil. A strong relationship was anticipated between the amount of time it takes a dry seed to imbibe water and the water content and hydraulic conductivity of the soil. However, in the research reports listed in Table 2, large differences in soil water matric potential and hydraulic conductivity produced little or no difference in either the rate of water imbibition by the seed, or the time for it to complete germination and subsequent seedling emergence. These results are puzzling, given the assumption that liquid transport is the major mechanism for imbibition by seeds.

To develop a mechanistic model of liquid flow from soil to seed, not only must the rate at which liquid water can move to the seed be known, but also the extent of liquid contact between soil and a seed. Models of contact area have been developed based on theoretical ideas of what contact between seed and soil water films would be like. Collis-George and Hector (1966) estimated that, at field capacity (-0.03 MPa), about 1% of the surface of a seed is wetted when surrounded by soil aggregates of a diameter similar to the seed. However, they are careful to state that the assumptions and simplifications used to make the calculations are most accurate only very close to saturation (-0.001 MPa). Those assumptions include a lack of hysteresis, which means that a water bridge must form and be maintained, despite water content fluctuations near the seed. When a dry seed is introduced into a moist soil, the seed quickly dries the soil it touches, reducing local water films to very thin layers (Collis-George and Melville, 1975). These difficulties are often handled by modelling only very wet conditions and using very coarse media for a soil analogue (Hadas and Russo, 1974). Given the evidence and theoretical difficulties, it is safest to assume that liquid bridges contact a very small proportion of the seed surface under many field conditions.

Behaviour of water vapour in soil

Water vapour content in soil air remains very near 100% relative humidity over the entire range of soil water contents at which plants and other organisms thrive (Table 1). The question is, how quickly can air at 100% relative humidity supply water to an imbibing seed? Convection is limited in soil, so diffusion is the predominant transport mechanism of soil gases. Diffusion is the process of random relocation of molecules through their individual motions. Gaseous molecules travel at high speed (about $630\,\mathrm{m\,s^{-1}}$ at room temperature), but have frequent collisions with other molecules. As a result, it takes very little time for molecules to move short distances, but a considerable time to move longer distances. For example, diffusion of water in air is about ten times faster over a distance of 1 mm compared to 4 mm, and 100 times faster over 0.1 mm compared to 1 mm (Denny, 1993).

Water films covering soil particles are the source of vapour for diffusion to the seed. Seeds planted in soil experience very short soil-to-seed distances. Therefore, when attempts are made to estimate the capacity of seeds to imbibe water vapour, very short diffusion distances must be taken into account.

The problem of diffusion distance appears to have affected several attempts to estimate the capacity of seeds to imbibe water vapour. The commonly quoted dogma is that a sealed vessel containing liquid and gaseous phases will attain an equilibrium of saturated vapour above the liquid. This, theoretically, is correct,

Table 2. Examples of research where little differences in timing of germination, timing of seedling emergence or water imbibition by seeds were recorded over a range of soil water matric potentials that produced very different hydraulic conductivities

Research report	Matric potential range (MPa)	Soil	Seed[a]
Pawloski and Shaykewich (1972)	-0.08, -0.53, -0.78	2 soils with 10 × conductivity difference	Wheat
Hadas and Russo (1974)	(1000 × conductivity difference)	Coarse sands	Pea, chick pea, vetch
Lindstrom *et al.* (1976)	-0.1 to -0.8	Silt loam	Wheat
de Jong and Best (1979)	-0.03, -0.60, -1.0	Sandy loam to heavy clay loam	Wheat
Rogers and Dubetz (1980)	-0.03, -0.5, -1.5	Sandy loam, clay	Wheat
Collins *et al.* (1984)	-0.015, -0.12, -0.5	Sand	Maize
Bouaziz and Bruckler (1989)	0 to -0.9	Clay loam	Wheat
Lafond and Fowler (1989)	-0.03 to -1.5	Clay loam	Wheat
Livingston and de Jong (1990)	-0.02 to -0.2	Sandy loam	Wheat, rapeseed
Blackshaw (1991)	-0.03 to -1.53	Sandy clay loam	Wheat, rye, canola, *Bromus tectorum*
Studdert *et al.* (1994)	-0.001, -0.2, -1.5	Silty clay loam	Wheat

[a] Wheat, *Triticum aestivum* L.; pea, *Pisum sativum* L.; chick pea, *Cicer arietinum* L.; vetch, *Vicia sativa* L.; maize, *Zea mays* L.; rapeseed, *Brassica campestris* L. and *Brassica napus* L.; rye, *Secale cereale* L.; canola, *Brassica napus* L.

but it is difficult to verify. When a dry seed is introduced into the air above the liquid, it is often assumed that the seed will be surrounded by an unlimited supply of vapour-saturated air. But because diffusion is quite slow over long distances, without significant convection currents there will be a gradient between a dry seed, at perhaps −100 MPa matric potential, and the 'vapour-saturated air' at nearly 0 MPa. As a result, a seed will germinate faster the closer it is to a water surface (Fig. 1).

In some studies, fairly short distances were used between the liquid water supply and imbibing seeds. In others, there were distances of from one to several centimetres, or the distance was not reported. Despite different methods and measurements, a comparison of research reports indicates a relationship between distance and estimated imbibition rate. Owen (1952) used a 1-mm air gap and reported that wheat germination was completed in 48 h at 20°C, about twice the time required in contact with liquid. Bruckler (1983) used a 1- to 6-mm air gap, and concluded that full imbibition of maize took three times longer in vapour than in liquid. Collis-George and Melville (1978) compared distances of 1 and 3 cm and measured 60 and 80 h for wheat germination to be completed. And, finally, Schneider and Renault (1997) placed maize grains 2 cm above water and concluded that it took ten times longer for them to imbibe in the presence of vapour than in liquid water. In all of these studies, diffusion distances were much greater than exist for a seed planted in soil, and therefore potential vapour flow was underestimated by many orders of magnitude.

Can vapour really be sufficient?

Few experiments have been conducted in which seeds have been intentionally germinated in vapour alone, although several reports exist where this has occurred while pursuing other goals. As mentioned earlier, Owen (1952) determined that wheat imbibed with vapour alone germinated in 48 h at 20°C, and Collis-George and Melville (1978) observed germination in vapour in 60–80 h. In addition, Etherington and Evans (1986) used sealed Petri dishes packed with soil to germinate various native seeds in contact with soil of different water contents. They found that a piece of fibreglass filter paper placed between the soil and a seed made it easier to observe the seed, and caused no noticeable delay in germination. These experiments demonstrate that liquid water is not required for timely germination.

Experiments designed to compare imbibition with and without seed–soil contact

In experiments where the behaviour of liquid was not producing an adequate explanation for water uptake, the involvement of vapour was offered as an explanation (Harper and Benton, 1966; Choudhary and Baker, 1982; Martin and Thrailkill, 1993). Rogers and Dubetz (1980) even concluded that vapour was apparently more important than soil texture, water content, bulk density and seed–soil contact in this phenomenon. The challenge is to demonstrate unequivocally that seeds at normal seed-to-soil distances, but without the possibility of liquid contact, can imbibe water at the same or nearly the same rate as seeds with soil contact.

An initial attempt to achieve this (Wuest *et al.*, 1999) involved a set-up very similar to that of Etherington and Evans (1986). Sealed Petri dishes, filled with soil at different moisture contents, were incubated at a range of temperatures. In some dishes, seed–soil contact was prevented by a piece of coarsely woven fibreglass cloth. This, necessarily,

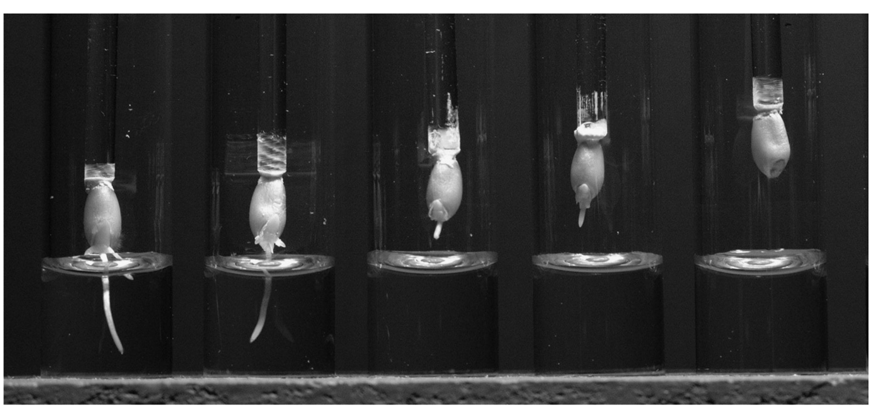

Figure 1. Wheat seeds suspended above water in sealed test tubes. A seed germinates faster (in 3 d) when it is closer to the liquid surface, demonstrating that diffusion of water through air is very dependent on distance. Distances range from *c.* 1 to 10 mm.

also increased seed-to-soil distance, but still there were comparable germination times with or without soil contact for wheat, barley, mustard and pea seeds (Fig. 2). This experimental set-up worked well for wheat and mustard, but barley appeared to suffer from compression of the lid in the soil treatment. The pea seeds were large and depleted the soil moisture in the Petri dishes to a greater extent than the smaller seeds. More refined methods should be used if this experiment is to be repeated, but the results demonstrate that seed–soil contact is not essential, or even important, for timely germination. When there is less water in the soil immediately surrounding the seed, it takes longer for seeds to imbibe the water they require, because it must be accumulated from a greater volume of soil; but it does not take nearly as long as the decrease in hydraulic conductivity would indicate (Table 1).

In the experiment, there were rare cases of water condensation on the inside surface of the lid of a Petri dish, but the condensation never touched a seed. Whenever condensation was observed, a circular patch of dry lid, several millimetres in diameter larger than the seed, surrounded where the seed contacted the lid. This probably indicates a zone around the seed where the vapour pressure gradient was steep enough to maintain less-than-saturated vapour conditions: a visual demonstration of the diffusion-limited vapour supply when liquid water is several millimetres from the seed.

A limitation of the above research design is the difficulty in proving that the fibreglass supplied absolutely no liquid water films to the seed. While fibreglass did not gain weight during the experiment or feel wet to the touch, nor did it pick up dyed water or transfer nitrate from the soil to the seed, microscopic liquid water films might have existed.

Thus, a different experimental design was devised (Wuest, 2002). A block of moist soil was formed containing many holes of different diameters to provide different seed-to-soil distances. Wheat grains were glued to plastic sticks (as in Fig. 1) and suspended in the holes. The soil contained a soluble dye, so it could be determined if a seed touched the soil, and the extent of seed-to-soil contact could be estimated. The diameter of the holes ranged from 2 to 13 mm. Since the wheat grain was approximately 3 mm in diameter, the seed-to-soil distance varied from a maximum of 5 mm to zero. Two positions in the soil block were without any hole, so the seed was forced directly into the block with intimate seed-to-soil contact. After 24 h, there was only a modest difference (about 15%) in water imbibition when comparing a seed-to-soil distance of 5 mm and intimate seed-to-soil contact (Fig. 3). Under similar conditions, wheat germinated in 40 h with seed–soil contact, compared to 55 h when suspended in the middle of an 11-mm hole. The approximately 30% faster germination might have been due to the difference in vapour diffusion rate over a 4 mm distance, compared to hundredths of a millimetre in the case of seed–soil contact. Nevertheless, contact with liquid water films

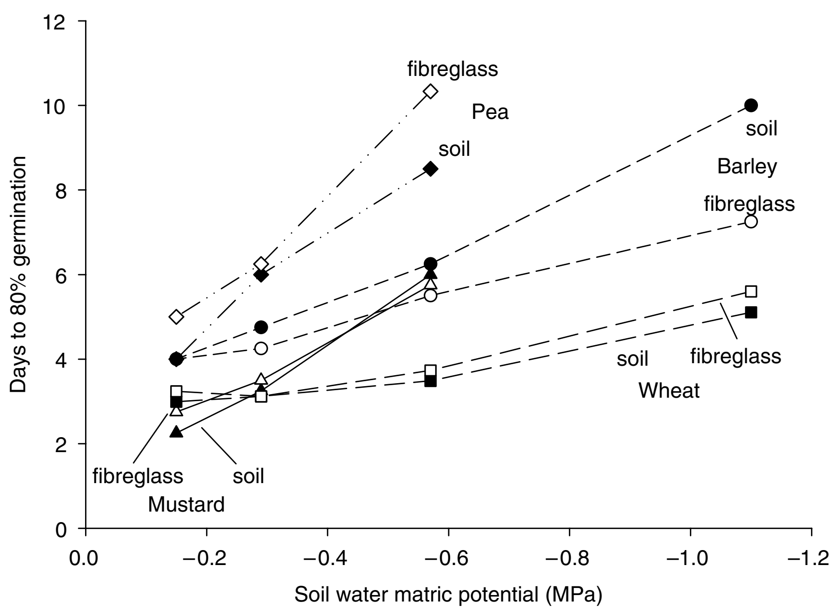

Figure 2. Number of days required for 80% seed germination of mustard, pea, barley and wheat placed in contact with soil (solid symbols), or separated from soil by a layer of fibreglass cloth (open symbols). Seeds and soil were sealed in Petri dishes and held at 16°C. Data for wheat are from Wuest *et al.* (1999); data for other species are previously unpublished.

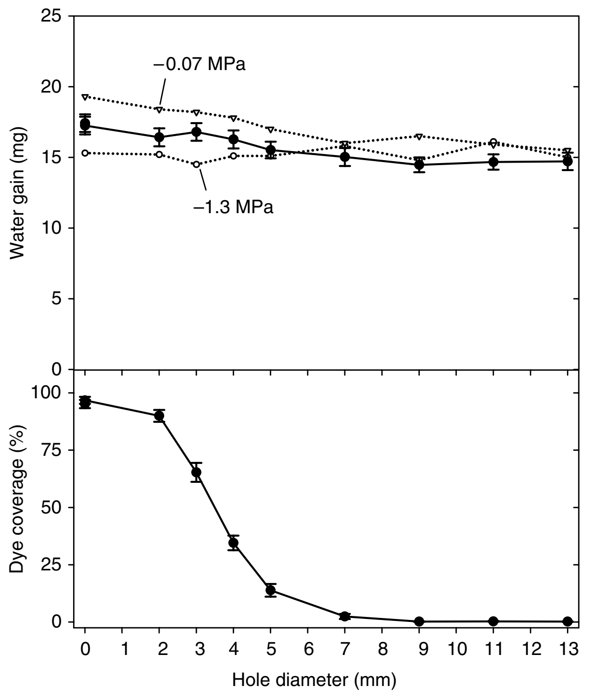

Figure 3. Average water gain and dye coverage (percent of seed surface) of wheat grains suspended in holes of different diameters for 24 h (solid lines). Error bars, where larger than the symbols, show standard errors of the mean ($n = 42$). There were two zero-diameter (no hole) positions in each soil block. Dotted lines indicate averages for the five experiments with the greatest soil water potential (−0.07 MPa) and for the four driest (−1.3 MPa). Average soil water potential for all 42 experiments was −0.16 MPa. From Wuest (2002); reproduced with permission of the *Soil Science Society of America Journal*.

was not essential for imbibition or germination, and lack of seed-to-soil contact only resulted in moderately delayed germination.

In laboratory set-ups such as that depicted in Fig. 1, or seed priming set-ups using osmotically controlled medium to partially imbibe seeds, conditions may be carefully controlled, but difficult to describe or verify accurately. Theoretical relationships between relative humidity and matric or osmotic potential are temperature dependent, and temperature gradients are likely. Collis-George and Melville (1978) measured a 2–3°C surface temperature rise for wheat grains, attributed to the heat of wetting and latent heat of condensation. (This is an alternative explanation for a lack of condensation on the Petri dish lids near a seed.) They concluded that unless this heat was dissipated, it would slow imbibition of vapour.

As permanent wilting point and critical water content for germination are approached, isothermal equilibrium relative humidity departs from 0.999 (Table 1). Given the effect of distance on gaseous diffusion and difficulty in detecting small temperature and humidity gradients, it may prove difficult to reconcile different germination results produced under different experimental methods when working near critical water contents.

Diurnal temperature fluctuations likely cause the soil atmosphere to fluctuate in relative humidity between supersaturated while cooling, and less than 100% when warming. This might result in liquid water condensation on the seed during cooling cycles. In terms of transport mechanisms, however, this would still be gaseous flux, independent of seed–soil contact. Lindstrom *et al.* (1976) compared constant temperature to 10°C diurnal fluctuation and found no difference in wheat emergence, so apparently diurnal temperature fluctuation produces no net increase of vapour to the seed.

Conclusions

An immediate practical implication of these observations is that planting methods need not emphasize seed-to-soil contact, but should instead focus on creating a humid environment around the seed. Evaluations of packer wheels, used to firm soil behind seeding equipment, have concluded that better seed-to-soil contact created by the wheels usually does not improve germination (PAMI, 2000). A very light surface compaction has often proven better, presumably by reducing vapour loss from the seed zone.

In a saline soil, germination is improved when the soil is dry enough for vapour to dominate imbibition, reducing mass flow of salts to the seed (Livingston and de Jong, 1990). Some effects attributed to root or seed exclusion of solutes might rather be a lack of soil contact and absorption of water as vapour.

More detailed measurement of vapour imbibition will require careful experimental set-ups, where distances between liquid water films and the seed surface approach zero. Perhaps, a very thin hydrophobic seed coating with excellent vapour permeability would work. Present evidence clearly indicates that water vapour in the soil should be regarded as an important component of water transport to the seed, and that seed–soil contact cannot fully explain seed water uptake, particularly in soils that are not saturated.

References

Blackshaw, R.E. (1991) Soil temperature and moisture effects on downy brome vs. winter canola, wheat, and rye emergence. *Crop Science* **31**, 1034–1040.

Bouaziz, A. and Bruckler, L. (1989) Modeling of wheat imbibition and germination as influenced by soil physical properties. *Soil Science Society of America Journal* **53**, 219–227.

Bruckler, L. (1983) Rôle des propriétés physiques du lit de semences sur l'imbibition et la germination. I. Elaboration d'un modèle du système 'terre-graine'. *Agronomie* (Paris) **3**, 213–222.

Choudhary, M.A. and Baker, C.J. (1982) Effects of drill coulter design and soil moisture status on emergence of wheat seedlings. *Soil and Tillage Research* **2**, 131–142.

Collins, G., Stibbe, E. and Kroesbergen, B. (1984) Influence of soil moisture stress and soil bulk density on the imbibition of corn seeds in a sandy soil. *Soil and Tillage Research* **4**, 361–370.

Collis-George, N. and Hector, J.B. (1966) Germination of seeds as influenced by matric potential and by area of contact between seed and soil water. *Australian Journal of Soil Research* **4**, 145–164.

Collis-George, N. and Melville, M.D. (1975) Water absorption by swelling seeds. I. Constant surface boundary condition. *Australian Journal of Soil Research* **13**, 141–158.

Collis-George, N. and Melville, M.D. (1978) Water absorption by swelling seeds. II. Surface condensation boundary condition. *Australian Journal of Soil Research* **16**, 291–310.

de Jong, R. and Best, K.F. (1979) The effect of soil water potential, temperature and seeding depth on seedling emergence of wheat. *Canadian Journal of Soil Science* **59**, 259–264.

Denny, M.W. (1993) *Air and water: The biology and physics of life's media*. Princeton, New Jersey, Princeton University Press.

Etherington, J.R. and Evans, C.E. (1986) Technique for ecological studies of seed germination in relation to soil water potential. *Plant and Soil* **95**, 285–288.

Hadas, A. and Russo, D. (1974) Water uptake by seeds as affected by water stress, capillary conductivity, and seed–soil water contact. I. Experimental study. *Agronomy Journal* **66**, 643–647.

Hanks, R.J. (1965) Estimating infiltration from soil moisture properties. *Journal of Soil and Water Conservation* **20**, 49–51.

Harper, J.L. and Benton, R.A. (1966) The behaviour of seeds in soil. II. The germination of seeds on the surface of a water supplying substrate. *Journal of Ecology* **54**, 151–166.

Lafond, G.P. and Fowler, B.D. (1989) Soil temperature and water content, seeding depth, and simulated rainfall effects on winter wheat emergence. *Agronomy Journal* **81**, 609–614.

Lindstrom, M.J., Papendick, R.I. and Koehler, F.E. (1976) A model to predict winter wheat emergence as affected by soil temperature, water potential and depth of planting. *Agronomy Journal* **68**, 137–141.

Livingston, N.J. and de Jong, E. (1990) Matric and osmotic potential effects on seedling emergence at different temperatures. *Agronomy Journal* **82**, 995–998.

Martin, D.L. and Thrailkill, D.J. (1993) Moisture and humidity requirements for germination of surface seeded corn. *Applied Engineering in Agriculture* **9**, 43–48.

Owen, P.C. (1952) The relation of germination of wheat to water potential. *Journal of Experimental Botany* **3**, 188–203.

PAMI (2000) Does soil packing matter? Research Update No. 749. Humbolt, Saskatchewan, Canada, Prairie Agricultural Machinery Institute, Web site http://www.pami.ca/pdfs/reports_reasearch_updates/749_does_soil_packing_matter.pdf (accessed 22 November 2006).

Papendick, R.I. and Campbell, G.S. (1981) Theory and measurement of water potential in soil, organic materials, plants, seeds, and microorganisms. pp. 1–22 *in* Parr, J.F.; Gardner, W.R.; Elliot, L.F. (Eds) *Water potential relations in soil microbiology*. Madison, Wisconsin, Soil Science Society of America.

Pawloski, M.C. and Shaykewich, C.F. (1972) Germination of wheat as affected by soil water stress. *Canadian Journal of Plant Science* **52**, 619–623.

Rogers, R.B. and Dubetz, S. (1980) Effect of soil–seed contact on seed imbibition. *Canadian Agricultural Engineering* **22**, 89–92.

Schneider, A. and Renault, P. (1997) Effects of coating on seed imbibition: II. Effect of coating rates. *Crop Science* **37**, 1850–1857.

Studdert, G.A., Wilhelm, W.W. and Power, J.F. (1994) Imbibition response of winter wheat to water-filled pore space. *Agronomy Journal* **86**, 995–1000.

Wuest, S.B. (2002) Water transport from soil to seed: The role of vapor transport. *Soil Science Society of America Journal* **66**, 1760–1763.

Wuest, S.B., Albrecht, S.L. and Skirvin, K.W. (1999) Vapor transport vs. seed–soil contact in wheat germination. *Agronomy Journal* **91**, 783–787.

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